

# Variation and Sexual Dimorphism of Body Size in the Plateau Brown Frog along an Altitudinal Gradient

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**Abstract** Variation in body size and sexual size dimorphism (SSD) can have important consequences for animal ecology, behavior, population dynamics and the evolution of life-history traits. Organisms are expected to be larger in colder climate (i.e., Bergmann's rule) and SSD varies with body size (i.e., Rensch's rule). However, the underlying mechanisms are still elusive. The plateau brown frog (*Rana kukunoris*), a medium-sized anuran species with female-biased SSD, is endemic to the Qinghai-Tibetan Plateau (QTP). From 1797 m (Maoxiang'ping) to 3453 m (Heihe'qiao) in the eastern margin of the QTP, we surveyed 10 populations of *R. kukunoris* and collected phalanges and snout vent length (SVL) data for 258 adult individuals (199 males versus 59 females). Based on these data, we explored how body size and SSD varying along the altitudinal gradient and examined the corresponding effects of temperature. We found body size to be larger at higher altitude for males but not for females, with likely effects from the temperature on the variation in male body size. Sex differences in growth rates may be the main cause of the variation in SSD. Our results suggested that only males follow the Bergmann's rule and variation in SSD of *R. kukunoris* do not support the Rensch's rule and its inverse. Therefore, the variations of body size can be different between sexes and the applicability of both Bergmann's rule and Rensch's rule should depend on species and environment where they live.

**Keywords** Altitudinal gradient, Bergmann's rule, body size variation, Qinghai-Tibetan Plateau, *Rana kukunoris*, Rensch's rule, sexual size dimorphism

## 1. Introduction

Body size is important for understanding animal ecology, behavior, population dynamics and the evolution of life history of a species (Morrison and Hero, 2003; Roff, 2002). Spatial and temporal variation in intraspecific body size is the basis of evolution and adaptation to different environments (Chown and Gaston, 2010; Yom Tov, 2001). In addition, body size of species is considered to be

influenced by life history traits such as growth rate (Cohen and Alford, 1993) and age at sexual maturity (Morrison and Hero, 2003). Amphibians are sensitive to subtle changes in surrounding environments and temperature has been recognized as the major factor affecting their body size (Laugen *et al.*, 2005; Laugen *et al.*, 2002; Laurila *et al.*, 2002). As predicted in Bergmann's rule (Bergmann, 1848), organisms tend to be larger in colder climates than those in warmer climates. Bergmann's rule was originally detected in mammals (e.g., Ashton *et al.*, 2000; Blackburn *et al.*, 1999). Subsequently, it has been found in ectotherms, including amphibians (e.g., Ashton and Feldman, 2003; Olalla Tàrraga and Rodríguez, 2007). An generally adaptive explanation for Bergmann's rule is heat conservation in cold environment, but its underlying causes may be diverse and even elusive (Gardner *et al.*,

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2011; Stevenson, 1985).

Moreover, intraspecific difference in body size between males and females has been defined as sexual size dimorphism (SSD) that is likely a result of sexual and/or natural selection (Fairbairn, 1997). Sexual selection can affect SSD through intra-sexual competition or inter-sexual mate choice favouring larger or smaller size in one sex (Andersson, 1994) and SSD may arise through natural selection when the sexes evolve to utilize resources in different way (Székely *et al.*, 2000). Additionally, SSD also acts as a consequence of differences in age, growth rate and age at maturity between sexes (Fairbairn *et al.*, 2007; Monnet and Cherry, 2002). Rensch's rule predicts that SSD increases with increasing body size when males are larger than females (male-biased SSD), but SSD decreases when females are larger than males (female-biased SSD; Fairbairn, 1997; Rensch, 1950). In regards to Rensch's rule, interspecific patterns with male-biased SSD have frequently been confirmed across different taxa, while female-biased SSD attracts relatively fewer attention (Fairbairn, 1997; Liao *et al.*, 2014; Stuart Fox, 2009). In recent years, the intraspecific pattern of Rensch's rule have been examined (e.g., *Pungitius pungitius*) (Herczeg *et al.*, 2010), and focused on male-biased SSD. This may result from the fact that the positive selection on body size for females was stronger than that for males (Herczeg *et al.*, 2010; Teder and Tammaru, 2005). Although females were suggested to be larger than males in 90 % anuran species (Shine, 1979), SSD in amphibians always do not follow Rensch's rule (De Lisle and Rowe, 2013; Liao *et al.*, 2013, 2014).

The Plateau brown frog *Rana kukunoris*, a medium-sized anuran species with female-biased SSD, is endemic to the Qinghai-Tibet Plateau (QTP), which distributed from 700 to 4400 m a.s.l. (Chen *et al.*, 2011; Fei *et al.*, 2009). Male frogs prefer large females as mates and males discriminate between the sexes based on their release calls (Fei *et al.*, 2009). Although female fecundity is positively related to body size, females at higher altitudes do not produce larger clutch size with the reproductive strategy for producing high offspring viability rather than having massive clutches (Chen *et al.*, 2013a). The eastern margin of the QTP is unique for the steep variation of altitude from 1200 to 3800 m a.s.l. within 50 kilometers and harsh environmental conditions (annual mean temperature: 14.1–1.1°C; annual total precipitation: 1332–649 mm; frost-free period: 269–120 days; <http://www.maoxian.gov.cn/>; <http://www.ruoergai.gov.cn/>). Therefore, it is important for us to understand how a frog species may

adapt to a specific environmental conditions on the QTP.

In this study, we aim to: 1) explore how body size of *R. kukunoris* varies along the altitudinal gradient and the effect of temperature on body size; 2) examine whether age, growth rate and temperature affecting the variation in SSD, and 3) test both the Bergmann's rule and the Rensch's rule for *R. kukunoris*.

## 2. Materials and Methods

We surveyed 10 populations of *R. kukunoris* from 1797 m a.s.l. (Maoxiang'ping, Maoxian County) to 3453 m a.s.l. (Heihe'qiao, Zoige County) in the eastern margin of QTP (Figure 1). A total of 258 adult individuals (199 males versus 59 females) were collected from late March to early May 2014 (Table 1). Frogs were randomly caught by hand in their spawning habitats. We identified individuals as sexually-mature males and females if they displayed nuptial pads on the fore digits and had well-developed oocytes (through visible externally), respectively (Fei *et al.*, 2009). We measured body size (snout vent length; SVL) of each adult to the nearest 0.02 mm with digital calipers. The longest phalange of the hindlimbs was removed and stored in 10% neutrally buffered formalin for subsequent age determination. Altitude of each population was recorded in the field by the Magellan eXplorist 310 GPS and average annual temperature was extracted from the data of Hijmans *et al.* (2005).

Age was estimated following the method adopted by Liao and Lu (2010). Cross-section of 12 µm of the mid-shaft diaphysis of the second phalanx with the smallest medullar cavity was selected and mounted on glass slides. The lines of arrested growth (LAGs) were identified under a microscope by two persons with equal experiences with agreed criteria for characterization. Due to the distinct temperature cycles through the year within the study area, the number of LAGs corresponds to the age of frogs (Chen *et al.*, 2011). Since the phalanges were collected during the breeding season, we regarded the surface of the bone as an additional LAG (Lai *et al.*, 2005; Morrison *et al.*, 2004). According to the protocol of Wake and Castanet (1995), we identified the endosteal resorption of LAGs based on the presence of the Kastschenko line (KL; the interface between the endosteal and periosteal zones; Rozenblut and Ogielska, 2005).

The index of SSD was calculated as  $\log_{10}(\text{mean female size}) - \log_{10}(\text{mean male size})$ . The index of sexual age dimorphism (SAD; the difference between mean male age and mean female age) of each population was calculated as  $\log_{10}(\text{mean female age}) - \log_{10}(\text{mean male age})$  (Liao

*et al.*, 2014; Smith, 1999).

Sex differences in mean body size and age among populations were examined using the generalized linear mixed models (GLMMs) with SVL and age as dependent variables, sex as a fixed factor, and population as a random effect. To control the effect of age on body size, age was added as covariate together with the interactions of sex  $\times$  age and sex  $\times$  population. The significant sex  $\times$  age interaction would be suggestive of sex differences in growth rates and the significant sex  $\times$  population interaction would provide evidence for variation in SSD among populations. Pearson's correlation analysis was used to evaluate the relationship between body size and altitude as well as the relationships between SSD and age-at-maturity, sex ratio, altitude, SAD and temperature. Partial correlation analysis was also adopted to decrease the effect of age on body size. General linear model (GLM) was conducted for testing the relationships between body size and both temperature and altitude, with SVL as a dependent variable, sex as a fixed factor, temperature, altitude and age as covariates.

To test the Rensch's rule, we conducted a regression for body size of females versus males. Least squares regression is inappropriate for testing the allometry because it assumes that the independent variable (here female size) is measured without error (Fairbairn, 1997). The reduced major axis (RMA) slope can be estimated

as the ratio of male to female standard deviations (Sokal and Rohlf, 1995). Therefore, we used RMA regression of  $\log_{10}(\text{male size})$  against  $\log_{10}(\text{female size})$  using the population means to test the Rensch's rule. When  $\log_{10}(\text{female size})$  was plotted on the x-axis and  $\log_{10}(\text{male size})$  plotted on the y-axis, a slope larger than 1.0 provided evidence for Rensch's rule (Fairbairn, 1997). The RMA regressions were performed in RMA software (<http://www.bio.sdsu.edu/pub/andy/rma.html>; Bohonak and van der Linde 2004).

Our statistical analyses were performed in SPSS 19.0 software (IBM Corporation, Chicago). All variables were log-transformed to meet the assumption of normality of variances. All probabilities were two tailed, and the significant level was at  $P < 0.05$ .

This study did not involve endangered or protected species. All the animal operations were approved by the Institutional Ethical Committee of Animal Experimentation of Chengdu Institute of Biology, Chinese Academy of Sciences, and strictly complied with the ethical conditions by the Chinese Animal Welfare Act (20090606).

### 3. Results

Age at sexual maturity was 2–3 years across populations without difference between males and females (Table 1).

**Table 1** Studied populations of *Rana kukunoris* along an altitudinal gradient with body size (snout vent length; mean  $\pm$ SD) and age of males and females for each population respectively.

Population ID	Populations	Altitude (m)	Annual mean temperature(°C)	Male		Female		Age at sexual maturity (Male/Female)
				Snout vent length (mm)	Age (year)	Snout vent length (mm)	Age (year)	
L1	Maoxiang'ping, Mao county	1797	10.8	43.53 $\pm$ 3.88 <i>n</i> =34	2.97 $\pm$ 1.31 <i>n</i> =34	49.50 $\pm$ 5.42 <i>n</i> =3	4 $\pm$ 0 <i>n</i> =3	2/2
L2	Lianghe'kou, Mao county	2296	9.0	50.20 $\pm$ 5.83 <i>n</i> =17	2.65 $\pm$ 0.70 <i>n</i> =17	63.77 $\pm$ 7.81 <i>n</i> =4	3 $\pm$ 0 <i>n</i> =4	2/2
L3	Baila'hai, Mao county	2526	8.6	46.99 $\pm$ 5.90 <i>n</i> =19	3.37 $\pm$ 1.07 <i>n</i> =19	—	—	2/—
L4	Yanwo'cun, Mao county	2954	6.9	53.38 $\pm$ 3.99 <i>n</i> =27	3.44 $\pm$ 0.58 <i>n</i> =27	57.62 $\pm$ 7.77 <i>n</i> =5	3.20 $\pm$ 0.45 <i>n</i> =5	3/3
L5	Mouni'gou, Songpan county	2769	7.6	50.44 $\pm$ 6.21 <i>n</i> =6	3.67 $\pm$ 0.82 <i>n</i> =6	49.93 $\pm$ 6.45 <i>n</i> =8	3.38 $\pm$ 0.74 <i>n</i> =8	2/2
L6	Chuanzhu'si, Songpan county	3022	6.2	51.85 $\pm$ 2.76 <i>n</i> =21	3.19 $\pm$ 0.51 <i>n</i> =21	57.42 $\pm$ 2.90 <i>n</i> =5	3.80 $\pm$ 0.84 <i>n</i> =5	3/3
H1	Huahu, Zoige county	3448	1.5	46.10 $\pm$ 3.38 <i>n</i> =18	3.22 $\pm$ 0.43 <i>n</i> =18	52.11 $\pm$ 4.20 <i>n</i> =7	3.71 $\pm$ 0.76 <i>n</i> =7	3/3
H2	Heihe'qiao, Zoige county	3453	1.8	50.78 $\pm$ 3.42 <i>n</i> =27	3.59 $\pm$ 0.89 <i>n</i> =27	54.40 $\pm$ 6.61 <i>n</i> =11	3.64 $\pm$ 0.92 <i>n</i> =11	3/3
H3	Tangke, Zoige county,	3450	1.8	50.40 $\pm$ 3.97 <i>n</i> =25	3.68 $\pm$ 0.85 <i>n</i> =25	59.60 $\pm$ 5.98 <i>n</i> =6	3.50 $\pm$ 0.84 <i>n</i> =6	3/3
H4	Xiaman, Zoige county,	3450	2.0	47.34 $\pm$ 3.12 <i>n</i> =5	3.2 $\pm$ 0.45 <i>n</i> =5	49.54 $\pm$ 5.88 <i>n</i> =10	3.40 $\pm$ 0.52 <i>n</i> =10	3/3

Mean age of individuals differed among populations ( $Z = 10.71$ ,  $P < 0.01$ ) but not between sexes ( $F_{1,1,197.57} = 3.28$ ,  $P = 0.07$ ).

Body size significantly differed among populations ( $Z = 10.70$ ,  $P < 0.01$ ) and females were larger than males ( $F_{1,1,197.57} = 46.88$ ,  $P < 0.01$ ). When the effect of age ( $F_{1,197.57} = 11.11$ ,  $P = 0.01$ ) was controlled, body size still significantly differed among populations ( $Z = 10.68$ ,  $P < 0.01$ ) and between sexes ( $F_{1,1,197.57} = 43.26$ ,  $P < 0.01$ ). The significant sex  $\times$  age interaction ( $F_{2,1,197.57} = 13.22$ ,  $P < 0.01$ ) showed that the relationship between body size and age ( $\approx$  growth rate) differed between sexes. The significant interaction between population and sex ( $Z = 10.4$ ,  $P < 0.01$ ) indicated that the degree of SSD differed among populations. Moreover, both temperature and altitude had significant effects on body size (temperature:  $F_{3,254} = 41.54$ ,  $P < 0.01$ ; altitude:  $F_{3,254} = 52.72$ ,  $P < 0.01$ ). Males tended to be larger in higher altitude but not for females (males:  $r = 0.28$ ,  $P < 0.01$ ; females:  $r = 0.16$ ,  $P = 0.22$ ). These trends of body size along the altitudinal gradient were similar when controlling the effect of age (males:  $r = 0.23$ ,  $P = 0.01$ ; females:  $r = -0.18$ ,  $P = 0.17$ ).

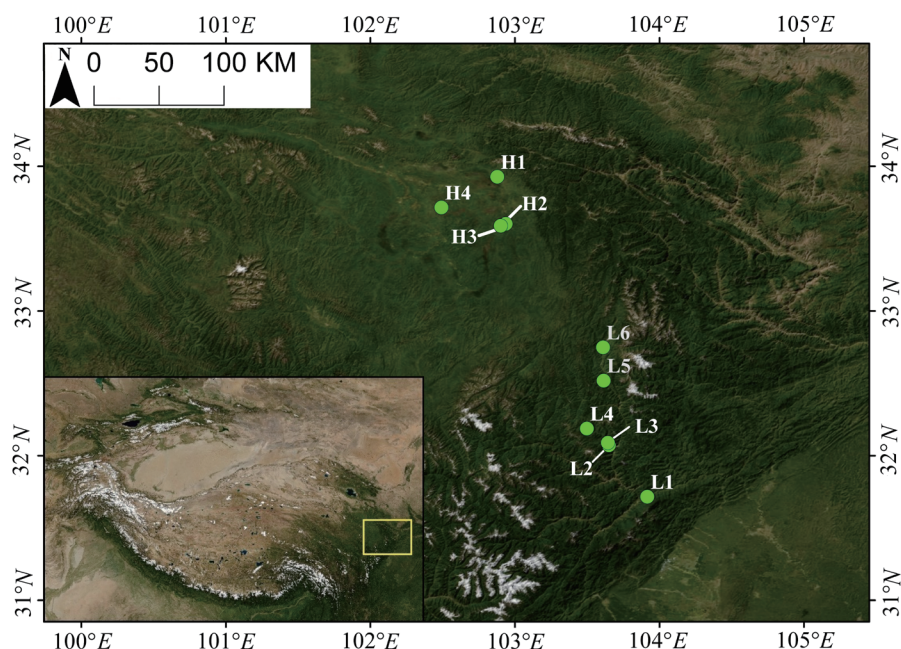
The degree of SSD did not correlate with age at sexual maturity ( $r = -0.15$ ,  $P = 0.69$ ), operational sex ratio ( $r = -0.01$ ,  $P = 0.99$ ), altitude ( $r = -0.30$ ,  $P = 0.43$ ), SAD ( $r = 0.41$ ,  $P = 0.27$ ) and temperature ( $r = 0.17$ ,  $P = 0.66$ ).

The slope of the RMA regression of  $\log_{10}(\text{male size})$  on  $\log_{10}(\text{female size})$  across populations was not significantly different from 1 (slope = 0.701, 95% CI = 0.21 – 1.20,  $R^2 = 0.379$ ,  $P = 0.071$ ).

#### 4. Discussion

For amphibians, variation in body size is frequently shown to follow the Bergmann's rule and is sometimes suggested to follow its inverse (e.g., Ashton, 2002; Iturra Cid *et al.*, 2010; Liao and Lu, 2010). For *R. kukunoris*, our results showed that the body size variation of males supported the Bergmann's rule, but not females (Figure 2). This is consistent with the different patterns of altitudinal variation in body size between sexes (Hsu *et al.*, 2014). Comparing with Chen *et al.* (2013a), we further found that the female body size tend to be constant along the altitudinal gradient. However, Chen *et al.* (2011) indicated that both males and females tend to be smaller at higher altitudes. This divergence may be induced by the different populations examined between this study and Chen *et al.* (2011).

Life history theory predicted that female body size is often related to fecundity (Monnet and Cherry, 2002). Fecundity hypothesis predict that female should invest more energy into somatic growth and delay sexual



**Figure 1** Study area and populations surveyed for *Rana kukunoris* along an altitudinal gradient in the eastern margin of the Qinghai-Tibetan Plateau. Circles represent populations surveyed. Capital letter H represents high altitude population, while L represents low altitude population. L1 represents Maoxiang'ping population; L2 represents Lianghe'kou population; L3 represents Baila'hai population; L4 represents Yanwo'cun population; L5 represents Mouni'gou population; L6 represents Chuanzhu'si population; H1 represents Huahu population; H2 represents Heihe'qiao population; H3 represents Tangke population; H4 represents Xiaman population.



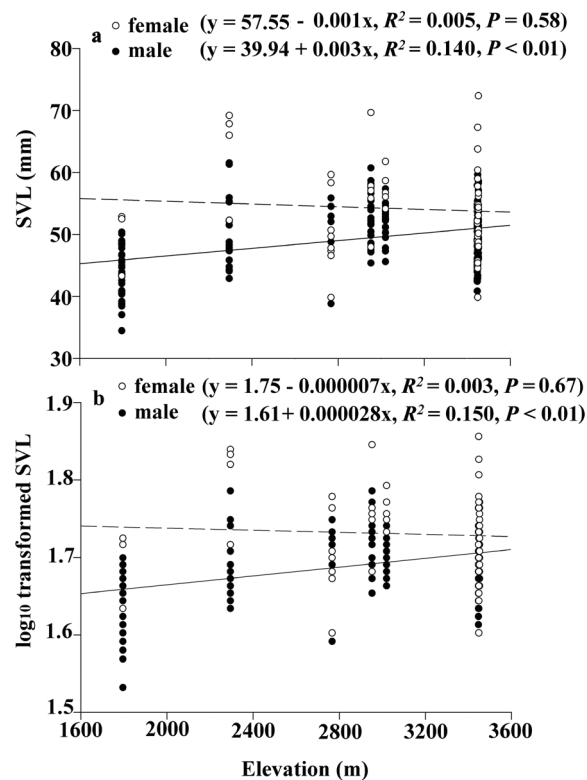
maturity to reach a larger body size and to attain higher fecundity (Iturra Cid *et al.*, 2010; Sinsch *et al.*, 2010). However, females' body size in this study did not vary among populations, and clutch size of them also did not increase with increasing altitude (Chen *et al.*, 2013a). Shorter activity time periods, combined with physiological limits on prey digestion may constrain female body size (Morrison and Hero, 2003; Roff, 2002). The fact that larger individuals may be unable to both recover energy spent on reproduction and store necessary energy to survive the coming winter (Chen *et al.*, 2013a) may explain why there was no altitudinal trend of female body size.

Body size can be strongly affected by environment conditions (Teder and Tammaru, 2005). For example, anurans at low temperatures grow slower towards the asymptotic body size and reach maturity later than those exposed to warmer temperatures (Morrison and Hero, 2003). In this study, the temperature gradient was not only the factor affecting the body size variation in *R. kukunoris*. At higher altitudes, the shorter activity time restricts the opportunity for energy accumulation. Hence, the frogs, especially females with a larger body size could be costly at higher altitudes, where shorter activity seasons restrict the amount of energy that an individual can accumulate and store prior to overwintering (Chen *et al.*, 2013b). Due to lower temperatures, individuals from higher altitudes reach sexual maturity later than those in lower altitudes. Moreover, higher ones could allocate more energy to reach larger body size (Morrison and Hero, 2003).

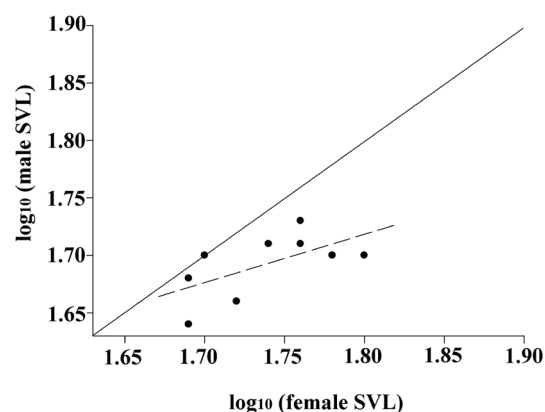
Sex differences in growth rate have potential effects on the variation in SSD (Fairbairn *et al.*, 2007; Monnet and Cherry, 2002). However, we find that variation in SSD among populations is significant when the effect of age is controlled and insignificant correlation relationship between SSD and SAD. These suggest that age or age structure is unlikely to explain variation in SSD for *R. kukunoris*. Moreover, differences in age at maturity, sex ratio, altitudes and temperature among populations could not explain variation of SSD as they were not correlated with SSD. In contrast, a significant difference in the relationship between body size and age of males and females across populations is found. This suggests that the differences in growth rates between sexes may explain the variation in SSD.

In *R. kukunoris*, variation in SSD do not support the Rensch's rule (Figure 3) as the allometric relationship between male size and female size is not significantly differed from the isometric relationship. This pattern has

also been found in other taxa with female-biased SSD (e.g., Liao *et al.*, 2013). A potential explanation for this is that fecundity selection on females favoring size balances



**Figure 2** Linear regression of snout vent length (SVL) on altitude for *Rana kukunoris*. a) raw data. b)  $\log_{10}$  transformed data. Each empty circle represents a female individual. Each filled circle represents a male individual. The dash line represents the regression of females. The solid line represents the regression of males.



**Figure 3** RMA regression of  $\log_{10}$ (male size) against  $\log_{10}$ (female size) across populations of *Rana kukunoris* [RMA regression equation:  $y = 0.4738 + (0.7012 * x)$ ,  $R^2 = 0.379$ ,  $P = 0.071$ ]. Each dot represents a single population based on the mean snout vent length (SVL) of females and males ( $n = 9$ ). The solid line represents isometry (slope = 1), while the dash line represents regression line (slope = 0.70).

rather than sexual selection in favor of larger males (Liao *et al.*, 2013). However, the limited sample size for females in this study may have effects on the insignificant results.

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